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DIFFERENTIAL ENHANCEMENT OF EARLY AND LATE COMPONENTS OF THE CEREBRAL SOMATOSENSORY EVOKED POTENTIALS DURING FORCED-PACED COGNITIVE TASKS IN MAN

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SUMMARY

1. Cerebral potentials evoked by random sequences of electrical stimuli to four fingers were recorded in intact man performing selective attention tasks. Eye movements and other artifacts were excluded from the averaged traces. Different finger stimuli were designated as targets to be mentally counted in alternate runs of each experiment. The high mean random rate of stimuli (150/min) fully involved the processing capacities of the subject. Vigilance changes or differential expectancy effects were excluded by the reciprocal random design with four different sensory channels. Task-related enhancements of somatosensory evoked potentials (s.e.p.) components were estimated by comparison with the s.e.p.s to physically identical finger stimuli recorded in runs when the subject attended signals in the opposite hand. The experimental design avoided subject's fatigue.

2. The primary s.e.p. components N_{20} and P_{45} were not significantly influenced and this excluded centrifugal gating of the corticipetal signals as a mechanism.

3. The earliest task-related changes in s.e.p. occurred 55–135 msec (mean 77·7 msec) after the target finger stimuli. In most cases the negative N_{140} component was markedly enhanced both for target signals and for non-targets in the adjacent finger of the same hand. However, in several subjects the targets elicited a positive P_{100} component instead. Both N_{104} and P_{100} were larger at the contralateral parietal focus than ipsilaterally. They were definitely smaller at the vertex and frontal scalp locations.

4. Enhancements of N_{140} were not observed in similar random four-finger experiments carried out at a 4 times slower mean rate, but they occurred in a bisensory paradigm with finger shocks and acoustic clicks at that slower rate.

5. A large positive P_{400} component was only elicited by target stimuli. Its voltage was maximum over the parietal region and was equal on both sides.

6. At least three categories of components can be differentiated in the cortical s.e.p. on the basis of their time domains (roughly 18–70 msec, 70 to 200–250 msec and over 200 msec after the finger stimuli), cerebral hemispheres topography and cognitive parameters. Verbal instructions defining specific perceptual tasks can to a large extent switch on and off the components of the second and third categories when the processing resources of motivated subjects are fully committed in a well designed forced paced paradigm. In certain individuals physiological evidence for a different 'stimulus set' processing of target (P_{100}) and non-target (N_{140}) signals was documented for the first time.

INTRODUCTION

Computer-averaged event-related cerebral potentials recorded from the intact human scalp offer a major opportunity for delineating the temporal features and spatial distribution of electrogeneses underlying conscious cognitive processes since it is only in man that specific perceptual tasks and verbal reports can be elicited. Scalp recordings monitor the activities of rather large sets of cerebral neurones, but they bypass the motor output and identify physiological features of sensory evoked potentials which can be controlled by psychological parameters (cf. Mackay, 1969; Donchin & Lindsley, 1969; McCallum & Knott, 1973; Callaway, 1975). For example task-relevant sensory stimuli which resolve the subject's uncertainty thereby allowing him to make a definite decision elicit a large positive component of 300–500 msec latency (P_{300}) which is related, not to the physical characteristics of the sensory stimuli, but to cerebral processing functions (Sutton, Braren, Zubin & John, 1965; Desmedt, Debecker & Manil, 1965; Chapman & Bragdon, 1965, Debecker & Desmedt, 1966; Donchin & Cohen, 1967; Vaughan & Ritter, 1970; Hillyard, Squires, Bauer & Lindsay, 1971; Tueting, Sutton & Zubin, 1971; Ritter, Simson & Vaughan, 1972; Donchin, Kubovy, Kutas, Johnson & Herning, 1973). Expectancy effects such as the contingent negative variation of Walter, Cooper, Aldridge, McCallum & Winter (1964; cf. Karlin, 1970; McCallum & Knott, 1973) have recently been differentiated from the P_{300} component which appears related to a perceptual decision (Donald & Goff, 1971; Donchin, Tueting, Ritter, Kutas & Heffley, 1975; Desmedt & Debecker, 1977). Along this line, when threshold sensory stimuli are presented to a subject in a difficult detection paradigm (cf. Green & Swets, 1966), a P_{300} is elicited by the detected signals, but not by identical stimuli which have not been perceived (Hillyard *et al.* 1971; Paul & Sutton, 1972; Squires, Hillyard & Lindsay, 1973; Barrett, Halliday & Rudolf, 1977). Changes in components occurring before 200 msec have also been recently recorded for the auditory evoked potential (a.e.p.), namely an increase of negativity

with peak at about 100 msec and the properties of this N_{100} differ from those of the P_{300} (Debecker & Desmedt, 1971; Hillyard, Hink, Schwent & Picton, 1973; Schwent & Hillyard, 1975; Schwent, Hillyard & Galambos, 1976). Current progress in this field results from the use of more critically differentiated experimental designs and of improved recording methods which exclude from the averaged brain potentials interference from eye movements and other artifacts that were not properly controlled in earlier studies (cf. Donchin, Callaway, Cooper, Desmedt, Goff, Hillyard & Sutton, 1977).

The present paper analyses the features and cognitive parameters of early and late components of the somatosensory evoked potentials (s.e.p.s) elicited by weak electrical stimuli delivered at random to four fingers at a rather high mean rate. When the stimuli were delivered at rather large intervals in such intra-modality selective attention task, s.e.p. components before 200 msec did not change even though large P_{300} were elicited (Desmedt, Robertson, Brunko & Debecker, 1977). By using different and carefully adjusted stimulus rates and intensities we have now elicited significant increases in the early s.e.p. components. Task-modulated multichannel somatosensory responses are of particular interest because the earliest cortical events can be more readily identified in the scalp-recorded s.e.p. (Giblin, 1964; Desmedt, 1971; Cracco, 1972; Matthews, Small & Beauchamp, 1974) than for other sensory modalities. The main questions raised in this paper are: (1) what are the earliest task-related changes in the cortical s.e.p.; (2) are scalp distributions and asymmetries over the two hemispheres different for these early changes and for the P_{300}; (3) do these two sets of changes reflect different psychophysiological perceptual operations?

METHODS

A total of twenty-four successful experiments were carried out on seventeen normal unpaid adult volunteers of both sexes. The subjects were highly motivated to perform the decision tasks correctly; they included the experimenters themselves, members of the scientific staff and interested medical students. A number of proposed volunteers were excluded for one or more of the following reasons: inadequate motivation or sluggishmess in the psychological tasks, excess background alpha activity in the electroencephalogram (e.e.g.), or inability to properly relax so as to minimize eye blinks and muscle potentials interferences.

Sensory Stimulation. Electrical square pulses of 0.2 msec duration were delivered by a set of four solid state stimulators through isolating transformers (Disa 5K9445.3) to fingers of the two hands. Four pairs of Beckman Ag-AgCl cup electrodes filled with electrode jelly (Cambridge Instruments Ltd) were placed on the skin prepared by heavy rubbing with alcohol, and tightly fixed with adhesive tape to prevent any drying of the paste. The electrodes of any pair were fixed on one side of the finger at about 3 cm from each other. In some experiments, two pairs of electrodes were placed on either sides of the second finger, while in other experiments they were placed on the second and third fingers, in either hands. The latter condition made it

easier for the subject to differentiate target shocks to the second finger from non-target shocks to the third finger of the same hand.

The subjective threshold was estimated rather roughly by a method of limits and the intensity was adjusted at 1–2 mA above that value. The stimuli were chosen to be as weak as possible in order to make the decision task difficult, and to be judged roughly equivalent in the four fingers when the subject focused his attention on each finger in turn. A Hewlett-Packard probe model $IIII_A$ served to monitor the current intensities which had occasionally to be adjusted, say by 0·1 mA, when re-checking after each run the subjective clarity and equivalence of the different finger stimuli.

The stimuli were delivered in a random sequence on the different finger locations, and the intervals between any consecutive stimuli also varied at random between 250 and 570 msec. The intervals were generated by a circuit based on a beta ray emitter (Carmeliet, Debecker & Desmedt, 1971) and the trigger pulses entered a loop formed by four OR gate circuits with individual duty cycles generally of 15 msec. Each OR gate was connected to one of the four stimulators. When the duty cycles were equal for each gate, the fingers received a random sequence of stimuli with equal probability, thereby providing about 50 % target stimuli, say on the second finger, and 50 % non-target stimuli on the adjacent finger of the same hand. In some of the experiments the duty cycles of the gates were made unequal so as to provide about 20 % target stimuli and 80 % non-target stimuli. The reduced probability of targets can increase the voltage of the P_{300} component (Sutton *et al.* 1965; Ritter, Vaughan & Costa, 1968; Tueting *et al.* 1971; Donchin *et al.* 1975) but this did not eventually prove useful in this study since large P_{300} were recorded in the 50–50 % condition, and the 80–20 % condition provided too few target samples for averaging. The mean rate of stimuli received by the subject for all the fingers combined was 2·5/sec or 150/min. For any electrode pair on one finger, the mean frequency of stimulation in the 50–50 % condition was 37/min.

Since the intervals between successive stimuli were occasionally as short as 250 msec, the P_{300} component elicited by a target stimulus must have its later part somewhat distorted by the potentials evoked by the subsequent stimulus. However, this contamination was of limited significance because the successive intervals between stimuli varied at random over a rather large range: thus rather a few proportion of the samples included subsequent responses occurring before the peak of P_{300} and these responses were largely averaged out since they occurred at various latencies. Notice also that most records illustrated were averages of several hundred samples.

In thirteen of the experiments the subject's attention was made to shift from the somatosensory to the auditory modality. The random sequence also involved four different stimulations, namely target and non-target electrical shocks to adjacent fingers of one hand, and binaural acoustic clicks delivered through PDR-10 earphones. Clicks about 50 dB above subjective threshold were generated by 0·1 msec electrical pulses to the earphones. The intensity difference between target and non-target clicks was set between 6 and 10 dB to provide a reasonably difficult discrimination task.

Recording of cerebral potentials. Sterile stainless-steel needles 0·2 mm diameter were inserted into the scalp to the same length of 6 mm, and connected to differential amplifiers of 10 MΩ input impedance. The eleven derivations used were monitored on line on oscilloscopes and stored in an Ampex 14-channel FR-1300 FM magnetic tape recorder operated at 15 in./sec. The system bandpass (3 dB reduction) extended from 3 kHz to 0·05 Hz (or 3 sec time constant). Such high frequency fidelity was necessary to resolve the early components of the s.e.p. (Desmedt, Brunko, Debecker

& Carmeliet, 1974). The recording needles were compatible with the 3 sec time constant when used with a high impedance input stage and they provided steady base line conditions about 15 min after their insertion (Desmedt, 1977). Two channels of the tape recorder were used to write the time of occurrence of the four different stimuli and the codes for the different psychological tasks (Carmeliet, Debecker & Demaret, 1974) which allowed homologous trials in different runs to be read from the tape automatically with the appropriate circuitry.

The subjects were told to keep the eyes open and to fixate a point during each run; these precautions reduced, but did not eliminate phasic artifacts such as eye blinks. Therefore the taped data were as a rule edited off line to exclude from the averages each trial in which any of the channel presented eye movements or blink artifacts, bursts of muscle potentials or amplifier blocking (Debecker & Carmeliet, 1974; Desmedt, 1977). The brain potentials were averaged on a Nicolet 1074 digital computer (4096 words of 9 bits) in the 4-channel mode with analysis times usually set at 250 or 600 msec, which provided a resolution of 4·1 or 1·71 points/msec respectively. The vertical electro-oculogram (e.o.g.) was recorded with Beckman cup electrodes fixed on the orbital ridge above and below the right eyeball and this was averaged under identical conditions after tape editing to check for absence of eye movement artifacts.

Our standard scalp derivations were the mid-line vertex and frontal positions (Cz and Fz according to the international 10–20 system; cf. Jasper, 1958), the left (F_3) and right (F_4) frontal as well as the somatosensory parietal hand projection which we take 3 cm behind C_3 and C_4 and call Sc (contralateral to the hand stimulated) and Si (ipsilateral to same). Additional electrodes were placed along the mid line or between F and S on the sides. Steel needles inserted about 10 mm into the left and right earlobes served as separate reference for the scalp electrodes on the same side in order to differentiate activities of the two hemispheres. The mid line scalp electrodes were referred to the right earlobe.

Procedure. The subjects sat comfortably in a reclining armchar in a sound-proofed, air-conditioned (24 °C, 50 % humidity) shielded room (Hougardy & Desmedt, 1967). About 40 min were required to set up all electrodes and familiarize the subject with the tasks. At least 8–14 runs of about 3 min each were then carried out in which the subject had to count mentally the target finger stimuli and to actively exclude from his mind the non-target stimuli to the adjacent finger and the shocks to the other hand. The number of targets counted was within 5 % of the number delivered in good performers. The subject relaxed and talked with the experimenter for 2–3 min between runs. The task involved different target stimuli of the same sequences in alternate runs so as to minimize trends related to extraneous factors. The experiment was discontinued when the performance became sub-optimal as indicated by inaccuracies in target counts, increasing incidence of eye blinks and background alpha in the e.e.g. or subject's complaint about difficulties to concentrate on the task which was indeed an exacting one.

Presentation of the data. The averaged potentials were written on paper by a Moseley *X-Y* plotter. Two s.e.p.s elicited by identical finger stimuli were superimposed which corresponded to different runs in which these stimuli either were targets to be counted (thicker traces), or were to be ignored by the subject who attended other stimuli. The thicker traces were obtained by writing the same trace 3 times, each time with a vertical shift by about 0·1 mm. The potential components were designated by considering their positive (*P*) or negative (*N*) polarity and their mean peak latency, for example N_{140} and P_{400}, thus following recent recommendations (Donchin *et al.* 1977). For the large positive component usually called P_{300} in the previous publications, we therefore used P_{400} because this was about the mean latency

of the peak of that component in the present study (Table 1). The use of the label P_{400} does not at all imply that we would be considering this component as different from the components designated as P_{300} or as P_3 by others.

RESULTS

Fig. 1 illustrates one of the bi-sensory experiments with random sequences of four stimuli, two electrical shocks to adjacent fingers of one hand and two binaural acoustic clicks with a 9 dB difference in intensity, so as to relate the present data to previous results. The auditory evoked potential (a.e.p.) presented a large increase of the negativity peaking at about 100 msec (N_{100}) at the frontal mid line electrode (Fig. 1*E*, *I*). The superimposed a.e.p. to identical clicks recorded in alternate runs when the subject counted finger stimuli shows that components preceding the N_{100} were not changed, but that a later positivity with a peak at about 400 msec (P_{400}) was elicited by the target clicks (Fig. 1*I*). The a.e.p.s simultaneously recorded at the parietal electrodes on both sides presented a later negative peak (N_{140}) and a larger P_{400} (Fig. 1*G*, *H*). The somatosensory evoked potential (s.e.p.) to target finger shocks presented large N_{140} and P_{400} components at the parietal electrodes, with little if any change of the early N_{20} and P_{45} components (Fig. 1*A*, *C* and *D*). As in each experiment the flat vertical electro-oculogram (e.o.g.) averaged under the same conditions and for the same trials provided a control that electro-ocular artifacts were absent (see Methods).

Fig. 2 shows a typical intra-modality experiment with random sequences of subjectively equivalent shocks to four fingers. Target stimuli to a designated finger elicited large symmetrical P_{400} components which were not seen in the control s.e.p.s to identical stimuli to the same finger of the left hand when the subject counted target shocks to the other hand (Fig. 2*B*, *C*). Non-target shocks to the finger adjacent to the one attended elicited only a very small late positivity (Fig. 2*E*, *F*) (Table 2). However the N_{140} appeared in the s.e.p.s to both target and non-target shocks in adjacent fingers of the same hand. The N_{140} were larger at the contralateral parietal electrode (*B*, *E*), where the primary components were present, than at the ipsilateral parietal electrode (*C*, *F*).

The P_{400} component is generally of maximal size over the parietal scalp (Vaughan & Ritter, 1970; Squires, Squires & Hillyard, 1975; Desmedt & Debecker, 1977). The topographical study of P_{400} to target finger stimuli showed that its peak voltage increased from frontal to central to parietal locations while the peak latency did not change (Fig. 3). In this experiment the control s.e.p.s to identical stimuli when the other hand was attended disclosed a virtual absence of P_{400} which indicated a rather powerful switching of that phenomenon by the task conditions (see also Fig. 2*B*, *C*). The

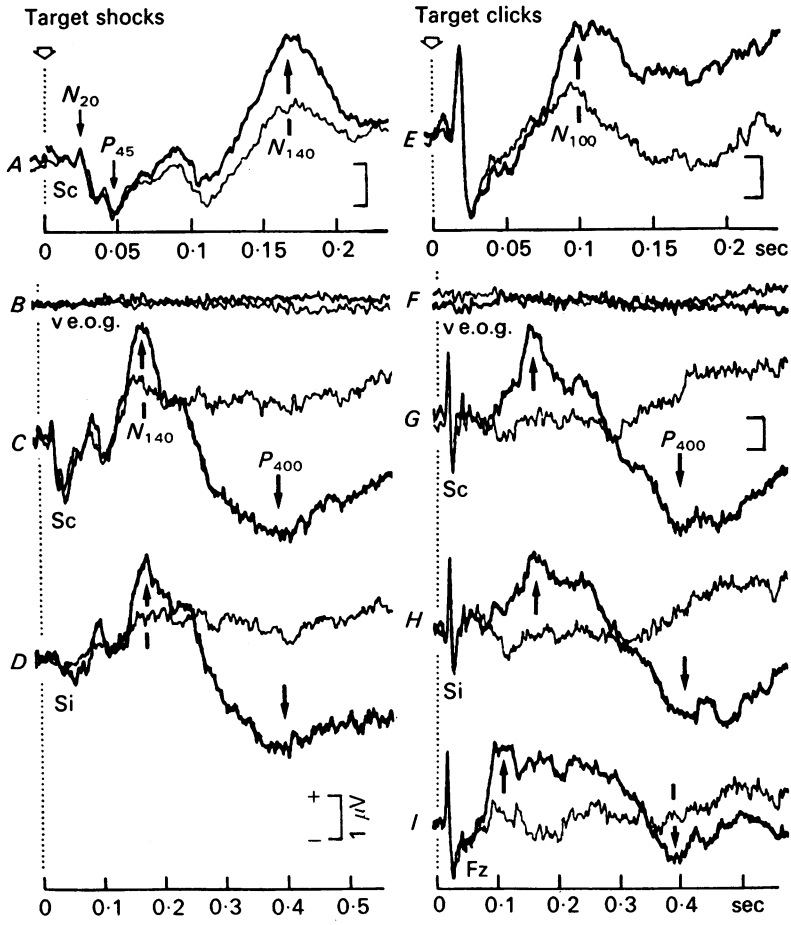

Fig. 1. Selective attention to either finger stimuli or to acoustic clicks. In all Figures, the superimposed traces correspond to potentials evoked at the same scalp location by physically identical sensory stimuli, under two different task conditions. *A–D*, s.e.p.s to electrical pulses of 3·5 mA to the third finger of the right hand when the subject attends that finger (thicker trace) or to target clicks (thinner trace), *A*, fast time scale showing no significant change in N_{20} and P_{45} components,) but an increase of N_{140} to target shocks. *B*, vertical e.o.g. controls. *C*, contralateral and *D*, ipsilateral parietal focus s.e.p.s showing large N_{140} and P_{400} to target shocks on a slower time base. *E–I*, a.e.p.s to binaural clicks of about 45 dB s.p.l. when the subject attends target clicks (thicker trace) or target finger stimuli (thinner trace). *E* and *I*, mid line frontal electrode (Fz) showing N_{100} and P_{400} to target clicks with two different time scales. *F*, vertical e.o.g. controls. The a.e.p.s to clicks recorded simultaneously at the contralateral (*G*) and ipsilateral (*H*) somatosensory focus present a later negativity N_{140} and a larger P_{400}. Negativity of the active electrode produces an upward deflexion. Number of trials averaged, $n = 600$.

P_{400} to targets had about the same voltage over the two hemispheres, thus at electrodes 6–8 cm from the mid line referred to the earlobe of the same side (cf. Fig. 8*B*).

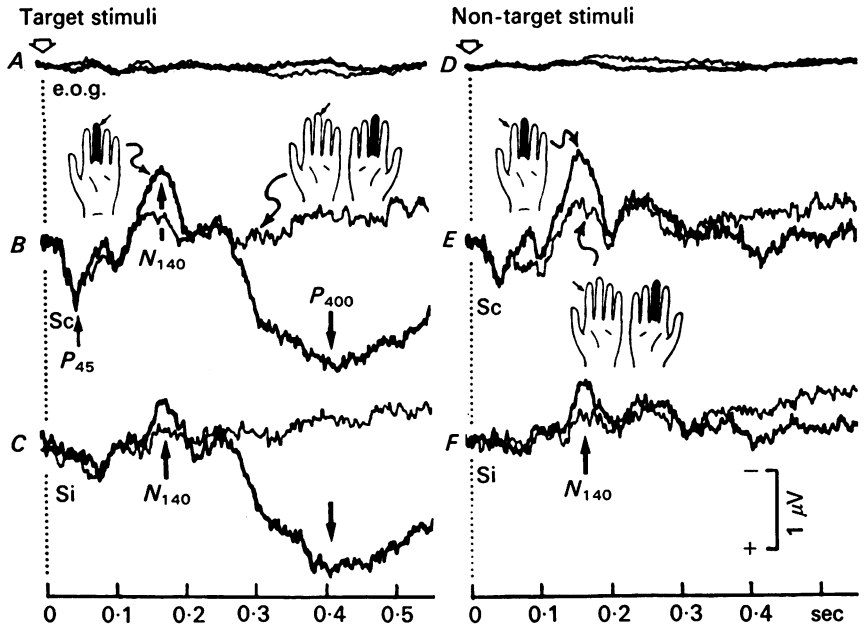

Fig. 2. Experiment with random sequence of stimuli to four fingers. *A* and *D*, vertical e.o.g. controls. *B* and *E*, s.e.p.s recorded at the contralateral paristal focus (Sc) by stimuli of 3 mA to the third (*B*) or second (*E*) fingers of the left hand. *C* and *F*, corresponding potentials recorded simultaneously at the symmetrical ipsilateral (Si) parietal electrode. The subject counts the target stimuli to the third finger of either the left (thicker traces) or the right hand (thinner traces). In the hand figurines, the attended finger is represented in black and the small arrow points to the finger stimulus which evokes the s.e.p. considered. N_{140} is larger contralaterally for both target and non-target stimuli to the left hand; P_{400} is symmetrical and only occurs for target stimuli. The early P_{45} components only appear contralaterally in *B* and *E* and they are not affected by the task. Trials averaged, $n = 560$.

TABLE 1. Features of s.e.p. components in the random fast four-finger paradigm (mean values ± S.D.). The number of experiments is indicated in parentheses

	P_{45} (19)	P_{100} (7)	N_{140} (16)	N_{400} (12)
Peak latency (msec)	46·3 ± 3·5	98·1 ± 4·6	151·4 ± 24	396 ± 41
Task-related increase in peak voltage (μV)	0·03 ± 0·24 (n.s.)	2·0 ± 0·8	1·8 ± 0·9	6·3 ± 5·8
Onset latency of these increases (msec)		69·4 ± 9·9	77·7 ± 28	

The scalp distribution of the early components is shown for two subjects in Fig. 4 where s.e.p.s to stimulation of adjacent fingers of the same hand have been pooled (to increase the number of trials in the averages) since the target and non-target s.e.p.s were highly consistent up to about 200 msec (cf. Fig. 2). The early components N_{20} and P_{45} of the s.e.p. are virtually restricted to the contralateral parietal focus (Fig. 4*B*, *I*), but

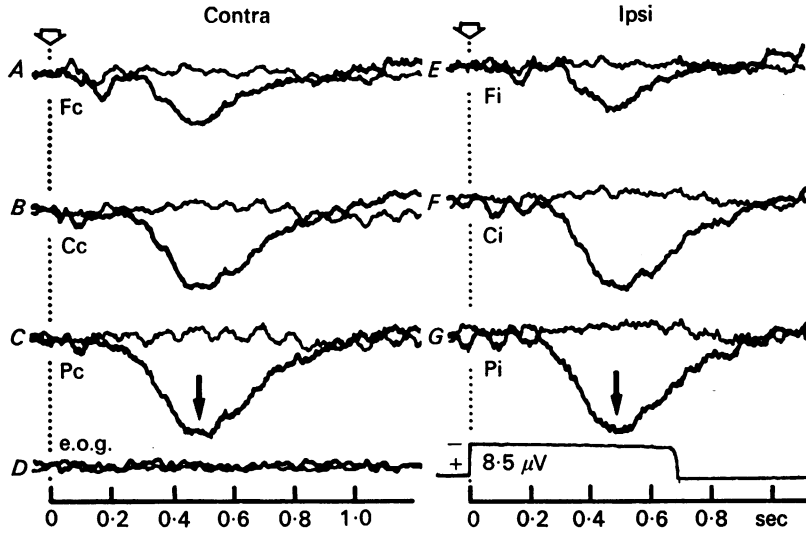

Fig. 3. Distribution of the P_{400} component to target finger stimuli. Shocks of 3·5 mA (1·5 mA above subjective threshold) delivered to four fingers. The s.e.p.s to target stimuli (thicker traces) are recorded simultaneously at frontal (*A*, *E*), central (*B*, *F*) and parietal (*C*, *G*) locations defined according to the international 10–20 system. The horizontal distance between each of these active electrodes was 6 cm. In this experiment the target stimuli had a mean probability of one fourth that of the non-target stimuli (see Methods). Left column, contralateral and right column, ipsilateral hemisphere. The thinner traces correspond to s.e.p.s identical finger stimuli when the opposite hand is attended. *D*, e.o.g. controls. Notice the bilateral symmetry and the perietal predominance of P_{400}. Calibration, step function of 8·5 μV. Trials averaged, n = 130.

the frontal electrodes disclosed a small early negativity which was symmetrically distributed (Fig. 4*E–G* and *L–N*) (cf. Cracco, 1972; Desmedt & Brunko, 1977). As in Fig. 1*A*, Fig. 2*B* and Fig. 5, the components N_{20} and P_{45} were not significantly changed by the task conditions (Table 1). The s.e.p.s to stimuli in the attended hand only diverge from the superimposed control s.e.p.s at about 55 msec in *B* and *I*, when the negativity leading to the N_{140} started to build up. The N_{140} peak occurred at about 165 msec for all the derivations of the second subject (Fig. 4*I–N*) and for

the parietal derivations of the first subject (*B*, *C*) in whom the frontal derivations presented an earlier peak at about 125 msec (*E*–*G*). The N_{140} peak voltage was about equal at the parietal derivations of both sides in the second subject (Fig. 4*I*, *J*), but larger contralaterally in the first

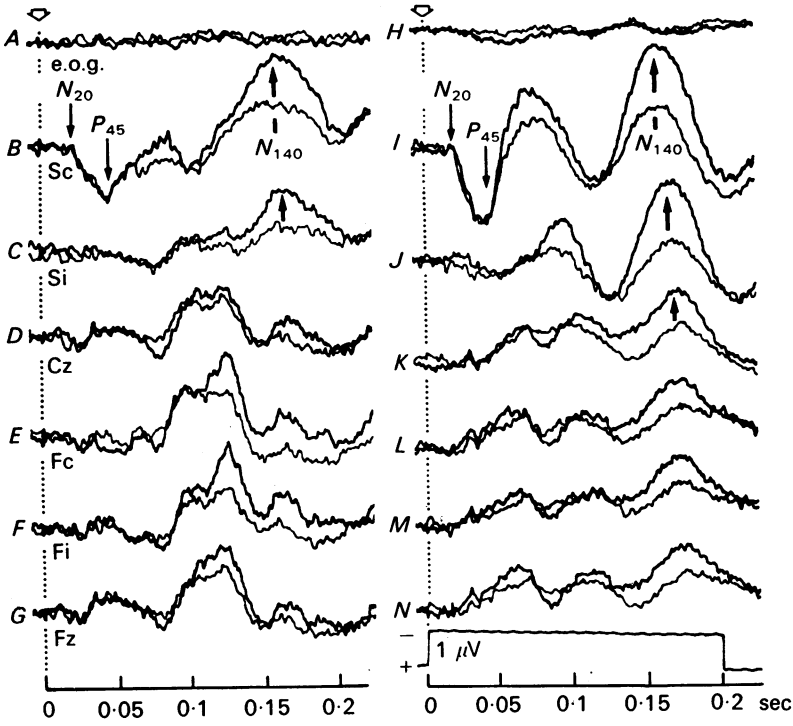

Fig. 4. Distribution of the early s.e.p. components in two different subjects. Random sequence of stimuli (3·5 mA for *A*–*G* and 3·0 mA for *H*–*N*) to four fingers. Thicker traces, pooled s.e.p.s target and non-target stimuli delivered to the hand attended. Thinner traces, pooled s.e.p.s to the identical stimuli when target stimuli in the opposite hand are attended. *A* and *H*, e.o.g. controls. Separate earlobe reference electrodes for the scalp derivation. *B* and *I*, s.e.p.s recorded at the contralateral parietal focus (Sc). *C* and *J*, symmetrical ipsilateral parietal derivations (Si). *D* and *K*, vertex derivation (Cz). *E* and *L*, contralateral frontal derivation which is 9 cm forward with respect to Sc. *F* and *M*, symmetrical ipsilateral frontal derivation. *G* and *N*, mid line frontal derivation (Fz). Calibration, step function of 1 μV. Trials averaged, $n = 2500$.

(*B*, *C*) who furthermore showed very little N_{140} at the vertex (*D*). The N_{140} voltage was about equal at the three frontal derivations. The onset latency of N_{140} to target finger stimuli was further examined with either the four-finger intra-modality paradigm at fast rates (Fig. 5*E*–*H*) (Table 1)

or the bisensory click-shock experiments at a slower rate (Fig. 5*B–D*). In both sets of data the earliest divergences in the negative direction ranged from 50 to 130 msec with a mean of 77 msec and there was no significant difference ($P > 0{\cdot}9$). There was apparently no tendency for

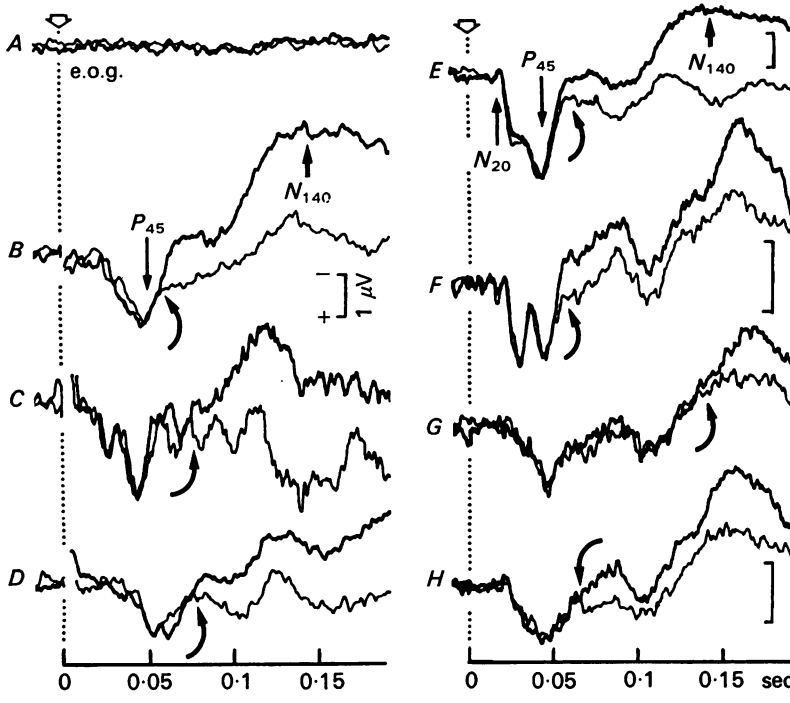

Fig. 5. Onset latency of the increased N_{140} to target finger stimuli. Superimposed s.e.p. to identical finger stimuli when this finger is attended (thicker trace) or when the subject attends either target clicks in *B–D* (over-all delivery rate of clicks and shocks 40/min) or, in other experiments, target finger stimuli in the opposite hand in *E–H* (over-all delivery rate of shocks to four fingers 150/min). The curved arrows point to the divergence of the two traces. Six different subjects are illustrated. Records *G* and *H* from the same subject represent s.e.p.s to stimulation of the second finger of either the right (*G*) or the left (*H*) hand. Calibration, 1 μV. Trials averaged, n = 400–1000.

longer onset latencies of N_{140} to occur in certain subjects since shorter and longer values were recorded for either hands in the same experiment on one subject (Fig. 5*G, H*). The unusually long latency of the early components in Fig. 5*D* was related to the use of small intensity threshold stimuli (cf. Desmedt *et al.* 1976).

Somewhat unexpected results were obtained for a few hands in which the

target stimuli elicited no N_{140} component, but instead an increased positivity with a mean peak latency of 98·1 ± 4·5 msec. These P_{100} components appeared at both contralateral and ipsilateral parietal electrodes and they were followed by large P_{400} (Fig. 6*A–C*). The mean onset latencies of the

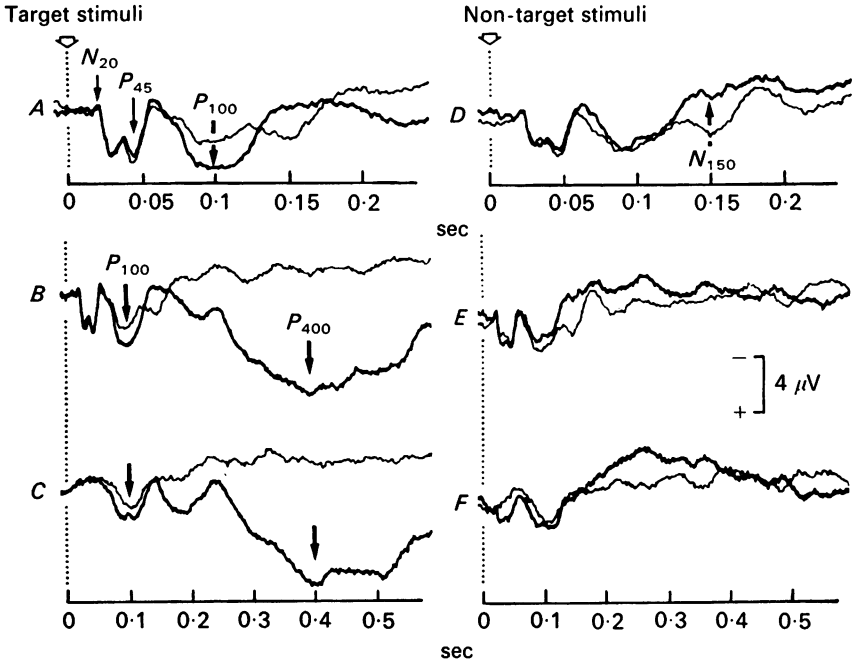

Fig. 6. Unusual task-related changes in subject K.L., in a four-finger experiment at fast rate. *A–C*, pooled s.e.p.s to all target stimuli of 3·5 mA to the second finger of either hands (N = 1050) recorded at the contralateral parietal focus with two time scales in *A* and *B*, and at the symmetrical ipsilateral location in *C* (thicker traces). The thinner traces correspond to s.e.p.s to identical stimuli when the subject is attending the opposite hand. The early components N_{20} and P_{45} are not changed, but the target stimuli elicit an increase in P_{100} and P_{400}. *D–F*, similar s.e.p.s to stimulation of the adjacent third finger when the subject attends that hand (thicker trace) or the opposite hand (thinner trace). *D* and *E*, contralateral parietal derivations. *F*, ipsilateral parietal derivations. Trials averaged, n = 1000.

P_{100} was 69·4 ± 9·8 msec. In this subject, the s.e.p.s to non-target shocks to the adjacent finger of the same hand did not show a P_{100}, but rather a small N_{140} (Fig. 6*D*) and they presented of course no P_{400} (Fig. 6*E*, *F*). Fig. 7 illustrates another subject disclosing a large N_{140} to target finger shocks in the left hand (*A*) and a large P_{100} to target shocks in the right hand (*G*). In this experiment the N_{140} was confined to the contralateral parietal focus

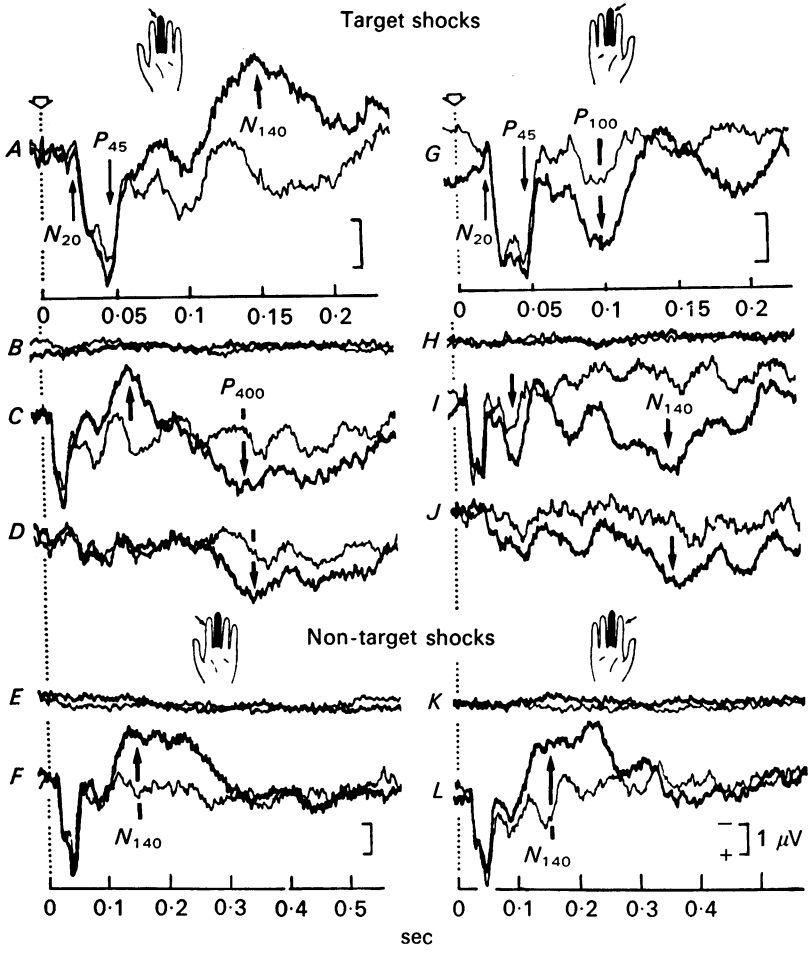

Fig. 7. Non-reciprocal task-related changes in the two hands of the same subject D.S. s.e.p.s to stimuli of 3 mA to the third finger of the left hand (*A–D*) or of the right hand (*G–J*) when these stimuli are targets (thicker traces), or when the opposite hand is attended (thinner traces). *B* and *H*, e.o.g. controls. The target shocks to the left third finger elicit a large N_{140} at the contralateral parietal focus (*A*, *C*), but none ipsilaterally (*D*). The target shocks to the right third finger elicit instead a P_{100} both contralaterally (*G*, *I*) and ipsilaterally (*J*). However, large N_{140} are recorded for non-target shocks to the adjacent second fingers of either the left (*F*) or the right (*L*) hands. *E* and *K*, corresponding e.o.g. controls. Number of trials averaged, $n = 450$. P_{400} are elicited by all the target shocks, but not by non-target shocks.

and absent ipsilaterally (Fig. 7*D*), even though equivalent P_{400} appeared on the two/sides (*C* and *D*). It is important to stress that the non-target stimuli to the adjacent fingers in the left (Fig. 7*F*) and right (*L*) hands

TABLE 2. Features of the N_{140} and P_{400} components elicited by either target or non-target (finger adjacent to target) stimuli in the random fast four-finger paradigm. The means ± S.D. are based on eight to twelve experiments. The difference is significant only for P_{400} task-related increase in voltage

	Target shocks	Non-target shocks	*t* test
Task-related increase of N_{140} (μV)	1·8 ± 0·9	1·7 ± 0·7	$P > 0{\cdot}8$
Peak of N_{140} (msec)	151 ± 24	147 ± 18	$P > 0{\cdot}6$
Task-related increase of P_{400} (μV)	6·3 ± 5·8	0·8 ± 1·8	$P < 0{\cdot}01$
Peak of P_{400} (msec)	396 ± 41	386 ± 39	$P > 0{\cdot}6$

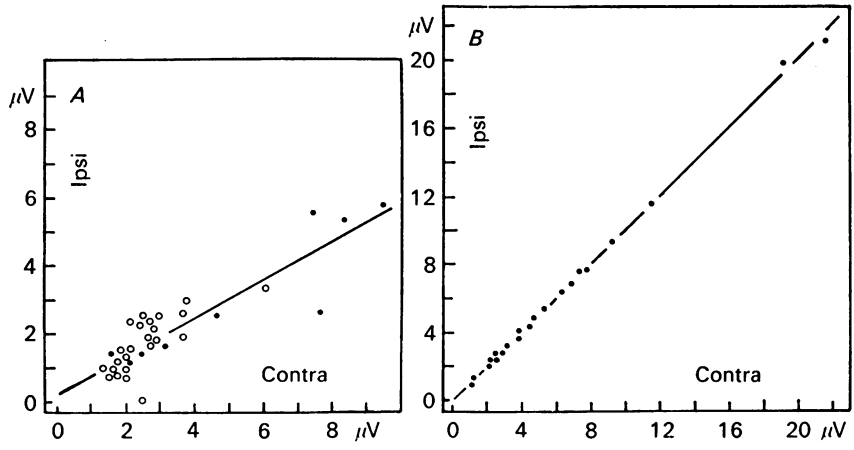

Fig. 8. Comparison of the peak voltages at symmetrical contralateral (abscissa) and ipsilateral (ordinate) parietal locations for task-related N_{140} (circles in *A*), P_{100} (dots in *A*) and P_{400} (dots in *B*) components. S.e.p.s to both target and non-target shocks are pooled in *A*. S.e.p.s to target shocks only are assembled in *B*. The voltages in μV are measured from the pre-stimulus base line. The N_{140} and P_{100} components are larger contralaterally while the P_{200} are symmetrical (see text).

elicited large N_{140} with no indication of any P_{100} component; there were of course no P_{400} to these non-targets. These data are important for showing that the P_{100} cannot be ascribed to some functional or anatomical anomaly of the somatosensory cortical projection of the right hand.

The pooled data of Fig. 8 compare the peak voltages of s.e.p. components simultaneously recorded at symmetrical parietal electrodes in all subjects for the four-finger paradigm. They disclose a significant contralateral predominance of both the N_{140} and the P_{100} components elicited by stimuli to the attended hand (Fig. 8*A*; $y = 0{\cdot}23 + 0{\cdot}55x$; $r^2 = 0{\cdot}79$). By contrast the P_{400} voltage was equal on both sides (Fig. 8*B*; $y = 0{\cdot}04 + 0{\cdot}99x$; $r^2 = 0{\cdot}99$).

DISCUSSION

Verbal instructions to the subject elicited different but highly consistent changes in the somatosensory evoked potentials (s.e.p.s) to identical electrical stimuli to a finger, either when these signals were designated as targets to be mentally counted, or when signals in the adjacent finger were counted, or when the task involved fingers in the opposite hand (Fig. 2). Alternate runs of the same experiment involved different target fingers in either the left or right hand: this reciprocal design provided an essential control that the enhancements of s.e.p. components were indeed switched on and off by focusing selective attention, and that they did not result from shifts in vigilance level or trends in the subject's involvement with the tasks. The parametric set was under better control than in other previous experiments in which a given stimulus was to be either attended or 'ignored'.

Experimental design of the cognitive tasks. The information load imposed on the subject can be increased by: (1) reducing the stimulus intensities closer to the subjective threshold (Hillyard *et al.* 1971; Paul & Sutton, 1972; Squires *et al.* 1973); (2) decreasing the interval between consecutive suprathreshold stimuli since simple decisions about clear signals can provide a considerable cognitive overload under forced-paced sequential stimulation (Debecker & Desmedt, 1970, 1971); (3) increasing the number of sensory channels to be monitored for the identification of targets (Schwent & Hillyard, 1975); (4) avoiding the warning cues which can either be deliberately provided at a fixed time before each target to facilitate detection (Fig. 7 in Desmedt *et al.* 1965; Barrett *et al.* 1977) or which can arise unintendedly in regular sequences of alternating stimuli (cf. Karlin, 1970). We are not concerned with threshold signal detection in which the decisions about ambiguous targets are variable and intermittent so that one requires a careful trial-by-trial checking of the actually detected stimuli by asking the subject to press a key; such motor responding is preceded by cerebral motor potentials (Bereitschaftspotential, see Kornhuber & Deecke, 1965; Deecke & Kornhuber, 1977) which we did not want to interfere with the s.e.p. Another problem with threshold targets is that P_{400} latencies present marked variations (Ritter

et al. 1972) and components can be blurred in the average record (Fig. 3 in Desmedt *et al.* 1977). Moreover, the primary components of the s.e.p. are rather small and less easy to evaluate with threshold stimuli.

Since the cognitive load of a task results from a trade-off between stimulus intensity, stimulus interval and number of channels, we used randomly intermixed sequences of four different stimuli 1–2 mA above subjective threshold and adjusted the required information load by reducing the random interval between stimuli. With random sequences of four shocks (rather than two alternating stimuli) the time of occurrence of the target finger stimuli was unpredictable (range of intervals 250–2280 msec; see Methods) and the subject's expectancy or readiness could not be geared to cues of the programme thereby preventing any differential preparatory states to be systematically associated with any one of the sensory channels (cf. Schwent & Hillyard, 1975). In many earlier experiments a complete randomization could not be instrumented and the simple alternating block design made it difficult to assess the independence of task-related components changes from non-specific expectancy effects.

The shock intensities were adjusted to elicit clear and equivalent sensations in the four fingers. The difficulty of the task was set by the forced paced conditions (Debecker & Desmedt, 1970) with mean random intervals of only 400 msec. Only highly motivated subjects could perform with less than 5 % error in the counts of each run and this ensured that the psychological requirements were indeed satisfied. The parametric set had to be critically adjusted for each subject: one useful criterion was that the shocks had to be weak but clear during the forced-paced overload, and that there was to be no doubt in the subject's mind as to whether any target stimulus had indeed been delivered when he attended the designated finger. Fatigue was avoided, the experiment being discontinued before the performance started to deteriorate.

Primary s.e.p. components and corticipetal input. Corticofugal inhibitory control of the sensory pathways are well documented but their role in perception is still far from clear (cf. Towe, 1973; Desmedt, 1975). The recently disclosed powerful gating by the thalamus reticularis nucleus (Skinner & Yingling, 1977; Yingling & Skinner, 1977) invites a closer search for possible changes in corticopetal input in selective attention sets. The s.e.p. to finger stimulation presents at the contralateral parietal focus clear early components which are virtually absent ipsilaterally (Giblin 1964; Desmedt, 1971; Cracco, 1972; Desmedt & Brunko, 1977) in view of their relation to the crossed lemniscal pathway (Halliday, 1967; Hazemann, Olivier & Dupont, 1969), and probably also because of the lack of callosal connections between the primary cortical areas for the hand in primates (Pandya & Vignolo, 1969; Jones & Powell, 1969, 1973). The

component N_{20} which is the first cortical event of the s.e.p. and the P_{45} were not significantly changed (Figs. 2, 4, 7; Table 1). The earliest s.e.p. enhancement was recorded 55 msec or more after the target finger shocks (Figs. 4, 5, 7; Table 1). Similar figures were observed in bisensory click-shock paradigms (Fig. 5*A–C*). The onset was certainly not earlier at the mid line or frontal scalp recording sites (Fig. 4). The mean onset latency of N_{20} to finger shocks is 18 msec in normal adults: it depends on the length of the arm and corresponds roughly to the conduction times in the faster axons of the peripheral and central afferent pathway (Desmedt, 1971; Matthews *et al.* 1974; Desmedt, Brunko & Debecker, 1976). Thus, for a period of about 50 msec (range 37–115 msc) from 18 msec after the finger stimulus, the cerebral s.e.p. presented identical features whether the signals were either actively attended or ignored. These data exclude both peripheral gating of the afferent volley (cf. Picton & Hillyard, 1974) and control of electrogenesis in the primary cortical area, but they leave it open whether delayed activation of thalamo-cortical loops of the type considered by Skinner & Yingling (1977) might be involved in switching the subsequent P_{100} or N_{140} cognition-related electrogenesis.

The N_{140} component. No enhancement of N_{140} was recorded in another random four-finger paradigm carried out at a much slower rate which indeed provided an easy task and allowed enough time for all the signals to be processed up to the stage of target recognition (Desmedt *et al.* 1977). That the attentional resources of the subject were not thoroughly mobilized under such conditions was introspectively evident; furthermore, when using slightly stronger finger stimuli, the obtrusive non-target finger signals then elicited smaller, but sizeable, P_{400} components (Desmedt *et al.* 1977). The present experiments with quadruple mean density of random signals in the concurrent finger channels imposed a more critical selective attention and improved the target selectivity of P_{400}. The large N_{140} in the s.e.p.s both to target and non-target signals in adjacent fingers of the attended hand (Fig. 2, Table 2) provided direct physiological evidence for a cognitive strategy in which earlier stages of the cerebral processing sequence were biased in relation to a definite effort of the subject; signals in the opposite neglected hand also became subjectively less conspicuous at these rates presumably because fewer attentional resources remained unemployed and thus occasionally available for the irrelevant channels. This interpretation is consistent with experimental psychology data suggesting that under forced-paced conditins, signals can be selected more efficiently if the brain processes are set to consider the sensory channels by which they arrive ('stimulus set') rather than to analyse one or more features of the signals for achieving each perceptual decision ('response set') (Broadbent & Gregory, 1964; Treisman, 1969). In the present study,

each of the four unescapable stimuli elicited action potentials in a number of skin and joint afferents (cf. Dawson, 1956) of different finger parts in the two hands. The corresponding signals can be considered as separate sensory channels since they had a definite local sign which was no doubt preserved up to the contralateral primary somatosensory cortex (cf. Woolsey, 1947; Anderson, Norrsell & Norrsell, 1972). However, during each run, the N_{140} was enhanced not only for targets but also for non-target signals in the adjacent finger, as if the 'stimulus set' conditions allocated in most cases (but see below) rather similar processing sub-routines for all signals from the attended hand.

An important finding is that the N_{140} electrogenesis involved cerebral areas quite asymmetrically. Related studies for the auditory modality suggested a centrofrontal mid line predominance of a negative component with peak at 80–120 msec (Picton & Hillyard, 1974; Schwent & Hillyard, 1975). Our results for s.e.p.s emphasize that N_{140} was about twice as large at the contralateral than at the ipsilateral parietal areas (Figs. 2, 4, 8*A*). It was even absent ipsilaterally in one experiment (Fig. 7*D*). N_{140} was definitely smaller at the mid line vertex, and also at the frontal scalp sites (Fig. 4). Asymmetries were not conspicuous frontally as they were parietally. The onset latency of N_{140} was shortest at the contralateral parietal site where the area (μV × msec) of increased N_{140} was also largest (Fig. 4). Thus task-related electrogenesis was rather widely distributed through cortico-cortical connections (cf. Jones & Powell, 1973) during the time domain between 55 and about 200 msec after the finger stimuli, but appeared to predominate in the contralateral parietal lobe.

The P_{100} *component.* In a few experiments the target stimuli to certain fingers elicited s.e.p.s with no N_{140}, but a P_{100} component instead. This cannot be ascribed to some cerebral anomaly since non-target signals in the adjacent finger elicited large (Fig. 7*K*) or moderate (Fig. 6*D*) N_{140} at the same contralateral recording electrode during the same runs. Moreover, the P_{100} feature, when present, was simultaneously recorded at the ipsilateral parietal electrode where its voltage was smaller (Figs. 6*C*, 7*J*, 8*A*). The parametric set for eliciting P_{100} appeared similar, P_{100} onset latency ranged from 55 to 77 msec (mean 69·4 msec). The task-related increase was about 2 μV for both N_{140} and P_{100} (Table 1). The reason why certain target signals elicited P_{100} are obscure and deserve a closer analysis. These data indeed provide the first evidence for a major difference in brain electrogenesis, and presumably in processing sub-routine, for target (P_{100}) and non-target (N_{140}) signals in the time domain beginning 55 msec after the stimuli, thus well before the onset of P_{400}.

Whereas N_{140} and P_{100} s.e.p. components appeared to be correlated with forced-paced selective attention tasks in the intra-modality random four-

finger paradigm, the N_{140} component of s.e.p. was consistently recorded even at slow rates in the bisensory click-shock experiments. Thus 'stimulus set' conditions appear to be organized by the brain when dealing with identification of signals in separate sensory modalities, but they would seem to be called upon during intra-modality selective attention tasks only when a cognitive forced paced overload is present. This finding opens up an important experimental strategy for the differentiation of task-related specific cerebral electrogeneses.

The P_{400} component. The present data agree with others in showing that a clear decision about an uncertain target signal is associated with a large P_{400} component starting 200–250 msec after the stimulus (cf. Sutton *et al.* 1965; Donchin *et al.* 1975). The virtual absence of P_{400} to non-target signals (Table 2, Figs. 2, 7) is also in line with previous results suggesting that a negative decision or correct rejection by the subject does not elicit a P_{400} (Hillyard *et al.* 1971; Paul & Sutton, 1972; Squires *et al.* 1973). Large P_{400} were elicited by target signals in this forced paced condition, but also in the previous series at slow rate in which no N_{140} was present (Desmedt *et al.* 1977) which confirms the differentiation between the sensory decision P_{400} and the earlier N_{140} component associated with 'stimulus set' processing strategy (cf. Hillyard *et al.* 1973; Schwent & Hillyard, 1975). In contrast with the definite hemispheric asymmetry found for task-related the N_{140} and P_{100} s.e.p. components, the P_{400} to target signals was symmetrically distributed in the right and left parietal areas (Figs. 2, 3, 8*B*) and obviously expressed a more diffuse electrogenesis of the posterior associative cerebral areas.

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